Stuttgarter Beiträge zur Naturkunde

Serie A (Biologie)

Herausgeber:

Staatliches Museum für Naturkunde, Rosenstein 1, D-70191 Stuttgart

Stuttgarter Beitr. Naturk.	Ser. A	Nr. 589	15 S.	Stuttgart, 10. 8. 1999

New Views on the Relationships among European Pleurocarpous Mosses

By Lars Hedenäs, Stockholm

With 2 figures

Summary

An overview is given of the results of higher level cladistic studies of pleurocarpous mosses, and the implications of these for the classification of severel larger families represented in Europe. Starting with the more ancestral taxa, the traditional Isobryales forms a basal grade, followed by another grade including taxa with capsules of *Brachythecium*-shape. The latter grade includes taxa such as the Brachytheciaceae, Ctenidiaceae, and Hylocomiaceae, as well as the subfamily Heterocladioideae of the Thuidiaceae. The Amblystegiaceae, Rhytidiaceae, the temperate members of the Hypnaceae, and the Thuidiceae (excl. the Heterocladioideae) form a monophyletic group, with the Plagiotheciaecae as their sister group. The few European members of the Callicostaceae, Hokeriaceae, Leucomiaceae, and Sematophyllaceae belong to another monophyletic group with mainly tropical and subtropical members. The tropical members of the traditionally heterogeneous Hypnaceae are not closely related to the temperate members found in Europe.

Zusammenfassung

Die Arbeit stellt die Ergebnisse einer Stammbaumanalyse der Großgruppen pleurokarper Moose und ihre Auswirkungen auf die Einteilung einiger größerer in Europa vertretener Familien dar. Wenn man mit den ursprünglichen Gruppen beginnt, stehen die Isobryales im herkömmlichen Sinn an der Basis, darauf folgen als weitere Verwandschaftsgruppe die Vertreter mit *Brachythecium*-artig gebauten Kapseln. Letztere umfaßt Gruppen wie die Brachytheciaceae, Ctenidiaceae und Hylocomiaceae sowie die Unterfamilie Heterocladioideae der Thuidiaceae. Die Amblystegiaceae, die Rhytidiaceae, die Vertreter der Hypnaceae in den gemäßigten Breiten und die Thuidiaceae (ausschließlich der Heterocladioideae) bilden eine monophyletische Gruppe, mit den Plagiotheciaceae als Schwestergruppe. Die wenigen europäischen Vertreter der Callicostaceae, der Hookeriaceae, der Leucomiaceae und der Sematophyllaceae gehören zu einer anderen monophyletischen Einheit, die hauptsächlich tropische und subtropische Vertreter aufweist. Die tropischen Vertreter der in der herkömmlichen Fassung heterogenen Hypnaceae sind nicht näher mit den Vertretern aus den gemäßigten Breiten, die in Europa zu finden sind, verwandt.

Contents

1. Introduction

The classification of pleurocarpous mosses into families and orders that we find in our current European floras (e.g., Frahm 1995, Frahm & Frey 1987, Nyholm 1960, 1975, Smith 1978) is very much based on the ideas of Fleischer (1900–1922) and Brotherus (1924, 1925). An attempt at refining the classification of pleurocarpous mosses was made by Buck & Vitt (1986), but their ideas basically agree also with those of Fleischer (1900–1922) and Brotherus (1924, 1925), as far as the larger patterns are concerned. The since long established family classification of pleurocarpous mosses has serious weaknesses which has been revealed in numerous papers dealing with different genera and families of pleurocarpous mosses. Studies of relevance to the European flora include those of Buck (1980, 1988), Buck & Crum (1990), Buck & Ireland (1985), Crosby (1974), Crum (1991), Enroth (1994), Hedenäs (1987a, b, 1989, 1997a), Miller (1971), Nishimura et alii (1984), Robinson (1986), Rohrer (1985a, b), and Whittemore & Allen (1989).

In a series of cladistic studies, the higher level taxonomic relationships among the pleurocarpous mosses were evaluated by the present author (Hedenäs 1994, 1995, 1997b, c, 1998a). These studies, as well as those of Hedenäs (1987a, 1989), suggest that the classification of the pleurocarpous moss families need to be changed in several important respects, and that their diagnoses need to be amended. The present paper is an attempt to summarise the taxonomic consequences of the results of these phylogenetic studies, as well as of other new data, for the classification of the European pleurocarpous mosses.

2. Characters and criteria for classification

Whatever method taxonomists use in inferring relationships and in classifying organisms they are ultimately depending on the interpretation of characters. The characters and their states are basically influenced by three factors (Harvey & Pagel, 1991), the phylogenetic history of a taxon, developmental factors (e.g., pleiotropy, developmental constraints), and environmental factors. Many character states are at present selectively neutral or their potential negative sides are outweighed by positive sides. These kinds of states may have been more positive in relation to the habitats of more ancestral taxa (e.g., Harvey & Pagel 1991, Wanntorp 1983). The phylogenetic history of species has been suggested to be of overwhelming importance for many character states (e.g., Hedderson & Longton 1996, Hedenäs & Kooijman 1996, Proctor 1984, Thiers 1988, Wanntorp 1983). However, character states where current environmental factors seem to be of more direct importance also exist, and there is clear evidence for the occurrence of important adaptations in response to current habitats. In pleurocarpous mosses the most important complex of characters showing this kind of adaptations is probably found in the sporophyte (e.g., BUCK 1991, CRUM 1972, GROUT 1908, HEDENÄS 1998b, PROCTOR 1984, SHAW & ROBINSON 1984, VITT 1981).

To separate different factors that influence character states is often difficult, but since our characters interpretation affects our interpretations of relationships this must be considered seriously. All character states where we can infer homology with other states should be included in a study. On the other hand, when we have strong evidence hat a large proportion of the similarities seen are analogous responses to certain environmental factors, as in numerous characters of specialised pleurocarp sporophytes (HEDENÄS 1998b), an uncritical use of such characters may lead to erroneous conclusions. Although overall patterns of character variation often reveals which states are truly homologous and which are not in a cladistic analysis (e.g., FOREY et alii 1992), when numerous characters evolve similar states in response to certain habitat factors this may lead to artificial groupings of taxa. An alternative may then be to exclude character state complexes with poorly understood homology relations until further research reveals which similarities are analogous (cf. HEDENÄS 1998b).

The system of FLEISCHER (1900–1922) and BROTHERUS (1924, 1925) were based on relatively few "key characters", such as the appearance of the vegetative leaf coasta, the shape of the median lamina cells, the presence or absence of leaf cell papillae and paraphyllia, and whether the shoots are flattened or not. Although they emphasised differences between unspecialised and specialised peristomes, they did not consider differences among unspecialised ones. The grouping criteria were usually overall similarity between species included in higher taxa, and the difference between apomorphous (derived) and plesiomorphous (ancestral) states were not considered. Frequently, more strongly derived taxa were placed in separate higher taxa with only a few species (e.g., *Myurella* in Theliaceae) to underline differences towards other species.

When analysing phylogenetic relationships with cladistic or phylogenetic methods, only synapomorphies (shared derived character states) within the studied monophyletic group are used as grouping criteria, while symplesiomorphies (shared ancestral states) are excluded since they do not provide any information regarding relationships within a group. As an example, the homogeneous leaf costa is a synapomorphy joining most pleurocarps. On the other hand, the plesiomorphic state of this character, a costa with differentiated stereids and guide cells, found in some basal pleurocarps is not joining these taxa with each other in a monophyletic group or suggesting that they belong to a monophyletic group together with the majority of the diplolepidous acrocarpous mosses with alternate peristomes which have the same state. However, symplesiomorphies may be informative at another taxonomic level and no characters can *a priori* be regarded as generally useless for phylogenetic inferences.

The most common way of polarising characters, that is, to establish which character states are plesiomorphous and which are apomorphous, is the outgroup method. To obtain credible results it is then important to find a suitable outgroup, and preferably the sister group, the group or taxon that is most closely related to the monophyletic group of interest, should be used. When it is difficult to know which is the sister group, and this is not a rare situation, it is common to chose several different outgroups that are considered likely to be relatively closely related to the study group. These outgroups can then be used both separately and jointly in the analyses. With the outgroup method the character states in the outgroup are considered plesiomorphous, and other states that are encountered in the ingroup are considered apomorphous.

A basic idea behind cladistic methods is that the simplest explanation for the occurrence of a derived character state in two (or more) taxa is that the state evolved once in their joint ancestor. To assume that the apomorphy evolved independently in the two taxa having them requires one additional evolutionary event than to assume that it evolved only once. According to the parsimony criterion we should settle for the evolutionary hypothesis requiring the smallest number of events to explain a certain pattern of character states within a group. If we prefer other explanations than the simplest, we must be able to explain the extra evolutionary events needed in a credible way, that is to add auxiliary *ad hoc* hypotheses. Such hypotheses are needed only to explain why the simplest explanation should not be accepted and are needed for each such case.

Thus, cladistic methods attempt to find the simplest possible solutions to the problem of which taxa are related to each other, or in other words they attempt to find the evolutionary tree having the smallest number of steps or character state transitions for a specific set of taxa and characters. In reality, the states of some characters are usually in conflict with each other, mainly because of the occurrence of analogous similarities (homoplasies) that were not detected prior to the analyses, or because the apomorphous states of some characters have reverted to the plesiomorphous ones. However, even if many characters are homoplastic and the same states appear in several groups in the phylogenetic trees, which is especially often the case when larger groups are studied, they should be included since these states may still be useful in group characterisations (cf. Bremer & Struwe 1992). What is important to remember is that the patterns of relationships found, when they are based on all available information and analysed cladistically with computer programs such as HENNIG86 or PAUP, are normally better founded than when our easily biased brains try to sort the enormous amounts of information involved. More information about cladistic methodology can be found in, e.g., Forey et alii (1992) or Mishler (1986). Because HENNIG86 or PAUP put limits regarding the number of taxa possible to include in a single analysis, one often has to approach larger groups stepwise. Thus, first the entire pleurocarpous moss group was analysed to find the major lineages, and then selected monophyletic groups identified in the first analysis were analysed in more detail.

3. Earlier classifications of some larger European pleurocarp families

Brotherus (1924, 1925) classified the pleurocarpous mosses into four orders (Tab. 1), of which the Eubryales also included acrocarpous taxa. Eubryales are not represented among the European pleurocarps and the Orthotrichineae belong to taxa that are basal to the main group of pleurocarps treated here (cf. Hedenäs 1994), and will not be discusses further here. The mainly tropical and subtropical "Hookeriales" and Sematophyllaceae have only a few representatives in Europe and will on-

Tab. 1. The ordinal and subordinal classification of pleurocarpous mosses by BROTHERUS (1924, 1925). Only families that include native European species with the circumscription of BROTHERUS are mentioned in the table.

Eubryales	Isobryales	Hypnobryales	Hookeriales
(only Extraeuropean pleurocarps)	Orthotrichineae Orthotrichaceae Ptychomitriaceae Fontinalineae Climaciaceae Fontinalaceae Leucodontineae Cryphaeaceae Hedwigiaceae Leucodontaceae Meteoriaceae Myuriaceae Neckerineae Neckeraceae Lembophyllaceae	Leskeineae Amblystegiaceae Brachytheciaceae Fabroniaceae Leskeaceae Theliaceae Thuidiaceae Hypnineae Entodontaceae Hylocomiaceae Hypnaceae Plagiotheciaceae Rhytidiaceae (incl. *Rhytidiadelphus* and *Loeskeobryum*) Sematophyllaceae	Hookeriineae Hookeriaceae

ly be mentioned when this is of relevance for other taxa. The main differences between BROTHERUS' (1925) Isobryales and Hypnobryales are found in the branching pattern, with a stronger tendency for dendroid or subdendroid plants in the Isobryales than in the Hypnobryales, and a more frequent occurrence of specialised sporophytes in the first than in the second order. Within Hypnobryales, BROTHERUS (1925) placed taxa which species have usually got single, long costae in the suborder Leskeineae, whereas those having double and usually short costae were mostly placed in the Hypninae. Thus, a few key characters related to the leaf costa were given a very strong weight in BROTHERUS' classification of pleurocarpous mosses. His placement of other families of relevance to the following is also indicated in table 1. BROTHERUS' four orders were recognised also by BUCK & VITT (1986; Fig. 1), their Bryales and Leucodontales corresponding to BROTHERUS' Eubryales and Isobryales, respectively. BUCK's and VITT's circumscriptions of the orders and subordinal taxa deviate somewhat from those of BROTHERUS (1924, 1925), for example in stressing differences between unspecialised and specialised peristomes more strongly at the ordinal level. For example, BUCK & VITT (1986) placed the Thamnobryaceae and Thuidiaceae in the Hypnales, and the Neckeraceae and Anomodontaceae in the Leucodontales (Isobryales). On the other hand, taxa with long, single costae and those with short, double ones were still basically kept in different groups within the Hypnales.

The since long established major groups in current classifications of European Hypnalean pleurocarps (e.g., AUGIER 1966, FRAHM 1995, FRAHM & FREY 1987, JENSEN 1939, NYHOLM 1960, 1965, SMITH 1978) depend to a high degree on the key characters of the leaf costa just mentioned. The reason why this classification has become so firmly stablished is probably that these costal characters are easily visible and present in the most frequently available generation, the gametophyte. However, at the same time it is obvious that this classification is based on a tiny portion of all

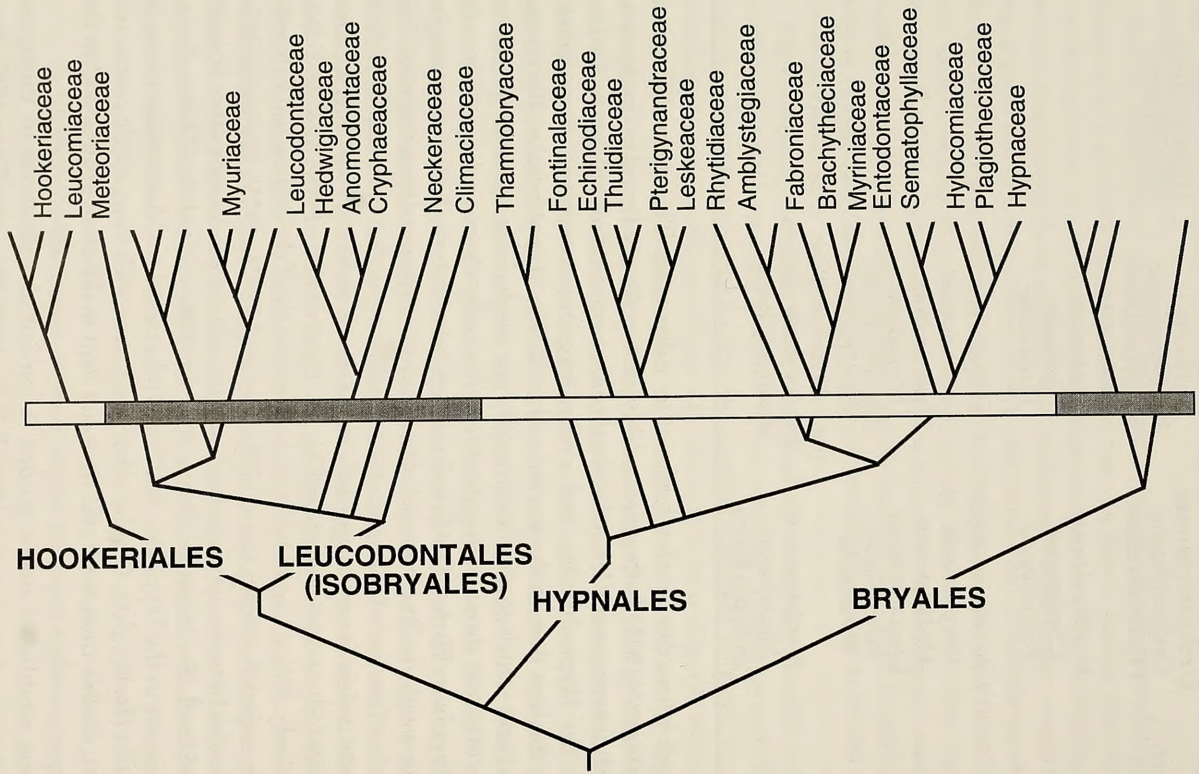

Fig. 1. Simplified summary of the phylogenetic relationships among the pleurocarpous mosses suggested by BUCK & VITT (1986), with families of interest to the present paper indicated. The extents of the traditional pleurocarp orders are indicated by grey and white portions of the transverse bar.

information potentially available in other characters. A partial exception is LIMPRICHT (1890–1895, 1895–1904), who classified the Amblystegiaceae together with the Plagiotheciaceae and Hypnaceae (including Ctenidiaceae and Hylocomiaceae) in his group Hypneae, separate from the Brachytheciae. If we look at some pleurocarp families having many members in Europe it is clear that the Hypnaceae has since long had the function of a catch-all family where species and genera of uncertain affinities were placed. This has caused an unclear circumscription of the Hypnaceae, and there has since long been a strong need to clear up its delimitations towards other families as well as the internal relationships. Two families of which the relationship to the Hypnaceae have caused much trouble are the Amblystegiaceae and the Plagiotheciaceae. Examples of different treatments of these two families are given in HEDENÄS (1998a: Tab. 3; Amblystegiaceae and temperate members of Hypnaceae) and in table 2 (Plagiotheciaceae). Roughly, members of the Amblystegiaceae have usually unicostate leaves and grow in moist or wet habitats, whereas the Plagiotheciaceae should include more or less complanate-foliate species with short double costae. However, some members of the Amblystegiaceae have also short, double costae like most taxa traditionally placed in the Hypnaceae, which makes the family circumscriptions obscure in many cases. The families Ctenidiaceae (incl. *Hyocomium*) and Hylocomiaceae are also often associated with the Hypnaceae, or they are frequently even included in the latter (NYHOLM 1965, NISHIMURA et alii 1984, SMITH 1978), and again the main similarity is found in the double costa.

Regarding the Hypnalean families which have members with mostly single costae, the delimitations between the Amblystegiaceae, Brachytheciaceae, and Thuidiaceae have sometimes caused trouble. The Brachytheciaceae are sometimes considered indistinctly delimited from the Ambylstegiaceae, and sometimes the main difference between them has been thought to be the wetness of the habitat where their species grow. Regarding the Thuidiaceae, there have been problems mainly with the delimitation towards the Leskeaceae (BUCK & CRUM 1990) and some members of the Amblystegiaceae, such as *Palustriella* (BUCK & CRUM 1990, OCHYRA 1989). Examples of different treatments of the European members of the Thuidiaceae are given in table 3.

Tab. 2. BROTHERUS' (1925), BUCK'S & IRELAND'S (1985), NYHOLM'S (1960, 1965), and SMITH'S (1978) placements of the European genera that were included in the Plagiotheciaceae by HEDENÄS (1987a, 1989, 1995) and PEDERSEN (unpublished data).

BROTHERUS	BUCK & IRELAND	NYHOLM, SMITH	HEDENÄS, PEDERSEN
Plagiotheciaceae	**Plagiotheciaceae**	**Plagiotheciaceae**	**Plagiotheciaceae**
Plagiothecium	*Plagiothecium*	*Herzogiella*	*Herzogiella*
Amblystegiaceae	**Hypnaceae**	*Isopterygiopsis*	*Isopterygiopsis*
Platydictya	*Herzogiella*	*Plagiothecium*	*Myurella*
Entodontaceae	*Isopterygium*	*Pseudotaxiphyllum*	*Orthothecium*
Orthothecium	*Taxiphyllum*	*Taxiphyllum*	*Plagiothecium*
Hypnaceae		**Amblystegiaceae**	*Platydictya*
Herzogiella		*Platydictya*	*Pseudotaxiphyllum*
Isopterygiopsis		**Entodontaceae**	**Position unclear**
Isopterygium		*Orthothecium*	*Isopterygium*
Pseudotaxiphyllum		**Theliaceae**	*Taxiphyllum*
Taxiphyllum		*Myurella*	
Theliaceae			
Myurella			

Tab. 3. BROTHERUS' (1925), NYHOLM's (1960), and SMITH's (1978) placements of the European genera that were included in the Thuidiaceae or Heterocladioideae by HEDENÄS (1995, 1998).

BROTHERUS	NYHOLM	SMITH	HEDENÄS
Thuidiaceae	**Thuidiaceae**	**Thuidiceae**	**Thuidiaceae**
Heterocladioideae	*Abietinella*	*Abietinella*	*Abietinella*
Heterocladium	*Anomodon*	*Anomodon*	*Anomodon*
Anomodontoideae	*Cyrto-hypnum*	*Helodium*	*Cyrto-hypnum*
Anomodon[A)]	*Haplocladium*	*Heterocladium*	*Haplocladium*
Claopodium	*Helodium*	*Thuidium*	*Helodium*
Haplocladium	*Heterocladium*		*Thuidium*
Euthuidioideae	*Thuidium*		**Heterocladioideae**[B)]
Abietinella			*Claopodium*
Cyrto-hypnum			*Heterocladium*
Thuidium			
Helodioideae			
Helodium			

A) Including *Haplohymenium.*
B) Not in the Thuidiaceae (cf. Tab. 4, Fig. 2).

4. Relationships suggested by the results of higher level cladistic analyses

The phylogenetic analyses by HEDENÄS (1995, 1997b, c, 1998a) suggest that the relationships between these families differ from the traditional ideas in many respects (Fig. 2, Tab. 4). First, the Isobryales does not form a monophyletic group (or clade), but consists of several monophyletic subgroups that have reached a certain level of development (a grade). The latter statement is here based solely on observations of the cladograms resulting from the phylogenetic analyses, and does not consider whether evolution is directional or not. Families such as the Leucodontaceae and Neckeraceae evolved within this relatively basal pleurocarp grade. Above the Isobryales grade follows another grade, consisting of taxa having spore capsules of the kind found in *Brachythecium.* Naturally, the Brachytheciaceae belong here, but also the Ctenidiaceae and Hylocomiaceae, which were earlier placed close to, or within the Hypnaceae, and the Heterocladioideae (with *Claopodium* and *Heterocla-*

Tab. 4. Suggested relationships between selected taxa that occur in Europe, based on the cladistic analyses performed by HEDENÄS (1995, 1997a, b, 1998a). See also Fig. 2.

Isobryales Grade	Brachtythecioid Grade	Temperate Clade	Tropical/Subtropical Grade	Tropical Clade
Echinodiaceae	Brachytheciaceae	Amblystegiaceae	Fabroniaceae	Callicostaceae
(incl. *Isothecium*?)	Ctenidiaceae	Hypnaceae	Myuriaceae	*(Cyclodictyon)*
Leucodontaceae	(incl. *Hyocomium*)	(temperate members)		Hookeriaceae
Meteoriaceae	Heterocladioideae	Plagiotheciaceae		Leucomiaceae?
Neckeraceae	Hylocomiaceae	Rhytidiaceae		*(Tetrastichium)*
		(only *Rhytidium*)		Sematophyllaceae
		Thuidiaceae		
		(excl. Heterocladioideae)		

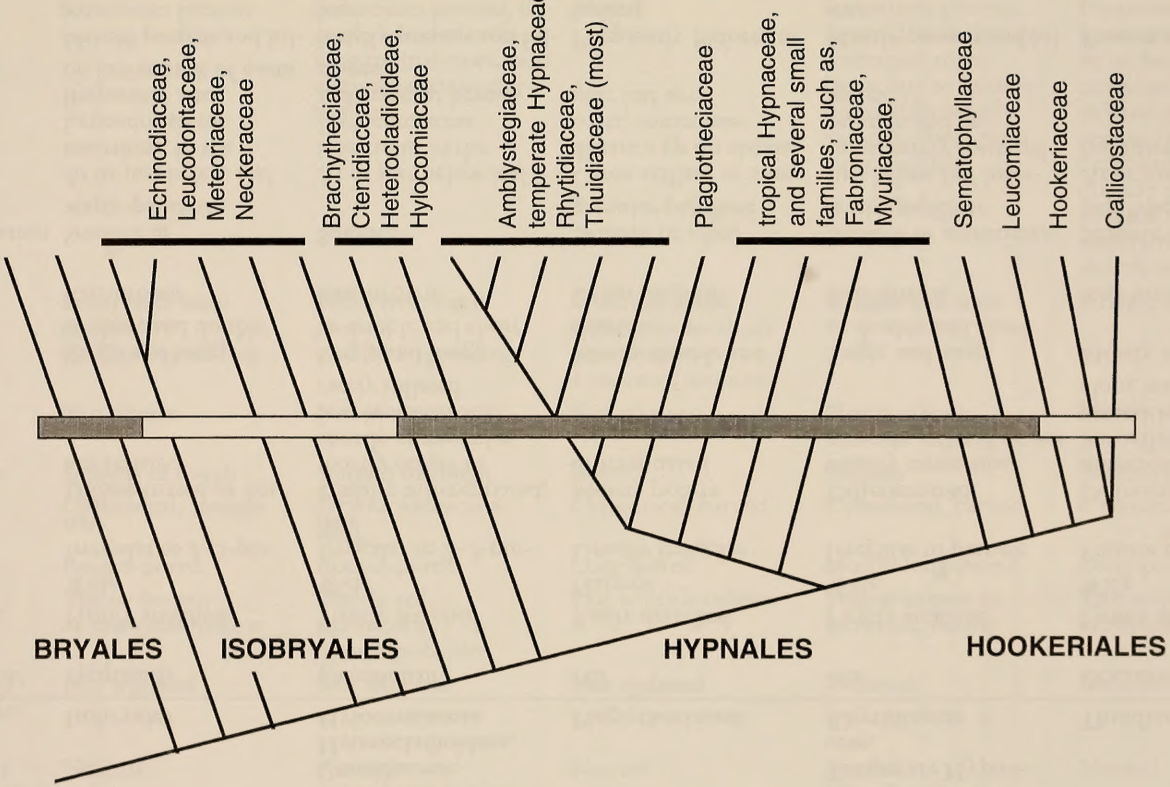

Fig. 2. Simplified summary of the results of the cladistic studies by HEDENÄS (1995, 1997a, b, 1998a), with selected taxa of interest to the European pleurocarp flora indicated (cf. Tab. 4). The thick horizontal lines above some terminal branches indicate clades or grades including the taxa mentioned above the lines. The extents of the traditional pleurocarp orders are indicated by grey and white portions of the transverse bar.

Tab. 5. The character states that are most frequent within some important pleurocarp clades or grades that are well represented in Europe (cf. Fig. 2). States of sporophyte characters refer to the condition in species with ± "horizontal" capsules and unspecialised peristomes. In "erect" capsules with specialised peristomes the character states are partly very different from those given, and in addition many similarities occur between taxa having specialised sporophytes in all five groups.

Characters / Taxa	Isobryales	Brachytheciaceae, Ctenidiaceae, Heterocladioideae, Hylocomiaceae	Plagiotheciaceae	Amblystegiaceae Temperate Hypnaceae, Rhytidiaceae	Thuidiaceae
Branching dendroid/ subdendroid?	Frequently	Occasionally	No	No	Occasionally
Branch attachment	Firmly attached	Firmly attached	Easily detached	Firmly attached	Firmly attached
Branching angle	Wide	Wide	Narrow	Wide	Wide
Branching pattern	Irregular to 2–3-pinnate	Irregular to 2–3-pinnate	Usually irregular	Irregular to pinnate	Pinnate to 2–4-pinnate
Alar cells	Differentiated or not, not inflated	Usually differentiated, mostly oblate to shortly rectangular, few or numerous, rarely inflated	Mostly poorly differentiated	Differentiated, usually numerous, strongly inflated or not	Differentiated, usually numerous, not inflated, extending far up along leaf margin
Leaf costa	Single and long, or short and double	Single and long, or double and short	Mostly double and short	Single and long, or double and short	Mostly single and long
Rhizoid colour (young)	Red-brown	Red-brown	Often purplish	Red-brown	Red-brown
Rhizoid ornamentation (young)	Smooth or warty-papillose	Smooth	Smooth or often granular-papillose	Smooth or sometimes warty-papillose	Smooth or warty-papillose
Rhizoid insertion	At or just below leaf insertions, in the Leucodontaceae frequently also on lower back of costa	At or just below leaf insertions, in the Hylocomiaceae axillary near branch apices	Often axillary or some distance up on abaxial costa, sometimes near leaf apex	Just below leaf insertions, rarely scattered on stem and on leaves*)	At or just below leaf insertions
Pseudoparaphyllia	Mostly present and foliose	Mostly present and foliose	Frequently filiform or lacking	Mostly present and foliose	Present and foliose

Paraphyllia	Sometimes present varying in shape	Sometimes present, diffusely inserted or in longitudinal rows, cells elongate-rectangular to linear	Absent	Sometimes present, inserted in obliquely transverse rows, lanceolate to ovate or linear, cells usually smooth, linear, with tapering ends	Frequent, often also on lower stem leaf margin or on back of lower costa, uniseriate or in basal part 2–3-(4)-seriate, frequently branched, cells frequently papillose or prorate, usually transversely rectangular to shortly rectangular
Inner perichaetial leaf orientation	From erect basal portion usually ± spreading	From erect basal portion usually ± spreading	Erect and small, sometimes suddenly narrowed to ± recurved acumen	Straight and erect	Straigth and erect
Inner perichaetial leaf plication	Not plicate	Not plicate	Not plicate	Mostly plicate	Mostly plicate
Seta ornamentation	Smooth or rough	Smooth or rough	Smooth	Smooth	Smooth or rough
Capsule shape	Cylindrical, straight	Of *Brachythecium* kind	Cylindrical, curved	Cylindrical, curved	Cylindrical, curved
Stomatal pores	Round-pored	Round-pored	Long-pored	Mostly long-pored	Long-pored
Exostome colour	Yellow-brown or brownish yellow	Mostly red, red-brown, or orange-brown	Pale whitish yellow	Yellow-brown or brownish yellow	Yellow-brown or brownish yellow
Exostome border at zone of transition in OPL pattern	Not widened	Not widened	Not widened	Widened	Widened or not
Endostome process width	Normal	Normal	Narrow	Normal	Normal
Endostome process perforation	Wide or narrow	Wide	Narrow	Narrow	Narrow
Spore maturation time	Winter half-year	Winter half-year	Summer half-year	Summer half-year	Summer half-year

*) The latter only in the *Calliergon-Scorpidium-Drepanocladus* complex.

dium), usually treated as a subfamily of the Thuidiaceae, evolved within this grade. In the more terminal parts of the pleurocarp cladogram, taxa of temperate regions, that in addition may occur at higher altitudes in tropical and subtropical areas, and taxa that are basically tropical or subtropical (lowland) are found in different clades or grades. In the clade with taxa from temperate areas we find the temperate members of the Hypnaceae, including the European species of this family, the Amblystegiaceae, the Rhytidiaceae, and the Thuidiaceae (except the Heterocladioideae) in the terminal clade, with the Plagiotheciaceae as its sister group. In the clade with tropical and subtropical taxa we find the few European members of the Callicostaceae, Hookeriaceae, Leucomiaceae, and Sematophyllaceae. Within a phylogenetic context, the "Hookeriales" cannot be recognised, unless many families, such as the Sematophyllaceae, are also recognised as orders. Likewise, the Bryales, Hypnales and Isobryales cannot be recognised as taxa in their traditional sense because they are paraphyletic (not including all descendants of their ancestor). Tropical members of the Hypnaceae, as well as many small families, for example the Fabroniaceae and Myuriaceae, are found in a grade at the basal regions of these two clades. It is noteworthy that most, perhaps all members of *Myurium* in the sense of Maschke (1976) are not related to *M. hochstetteri* (Schimp.) Kindb., but belong to other families, such as the Sematophyllaceae.

In the clade with the temperate members of the Hypnaceae, the Amblystegiaceae, most of the Thuidiaceae, and the Rhytidiaceae, only the Thuidiaceae form a monophyletic group, whereas the other families cannot be separated from each other based on morphological and anatomical characters (Hedenäs 1998a). The Thuidiceae have its root somewhere among the Amblystegiaceae-temperate Hypnaceae. The taxonomic consequences of these results, if later supported by, for example, molecular studies would be that at least the Amblystegiaceae and Rhytidiaceae should be merged in the Hypnaceae. Whether the Thuidiaceae should be regarded a specialised ingroup in the Hypnaceae or be recognised as a seperate own family is also depending on the results of further studies. Since the name "Hypnaceae" is bound to the basically temperate genus *Hypnum*, the temperate part of the family will keep this name. Most members of the present Hypnaceae from tropical and subtropical areas are thus not closely related to the temperate taxa. From this follows that the tropical taxa need to be completely re-evaluated, and that they should be excluded from the Hypnaceae. The Plagiotheciaceae will remain as a well circumscribed family, including a number of genera that were traditionally placed in several other families (Tab. 2).

5. Characters of importance in circumscribing the different groups

While earlier ideas suggested that relatively few characters were important for understanding and circumscribing higher level pleurocarpous taxa, the phylogenetic analyses suggest that numberous characters must be involved. The states of these characters are indicated in table 5. Although a few characters, such as leaf costa length and paraphyllia have frequently been used earlier in higher level classifications, many of them have newly turned out to be of importance for the circumscription of the taxa. The Plagiotheciaceae is a good example of a family where earlier ideas have proved to be misleading. Flattened shoots have turned out to be of very limited value in circumscribing this family, whereas characters related to rhizoids and exostome colour are most valuable (cf. HEDENÄS 1987a, 1989, 1995).

From table 5 it can be seen that for many characters one state is most frequent but still not universally occurring within a certain group, or the characters are homoplastic. This can be assumed to be due to parallel evolution of similar states that at present are inseparable by their appearance, but which is revealed in the cladistic analyses. This may seem slightly confusing at first, but since the phylogenetic analyses are based on all available characters this is still the best hypothesis regarding the relationships of the different groups that we can obtain. It also clarifies which characters and groups of taxa we need to study more thoroughly to be able to separate truly homologous from analogous structures. As was already mentioned, it should also be remembered that the states of these characters are still useful in the overall characterisation of the different groups (cf. BREMER & STRUWE 1992).

6. Acknowledgements

The present paper is based on studies financed by the Swedish Natural Science Research Council (NFR). The organisers of the BLAM-Jubiläumstagung are thanked for providing the means for attending and presenting this paper at the symposium in Stuttgart.

7. References

AUGIER, J. (1966): Flore des bryophytes. – Encyclopédie Biologique **44**: 1–702; Paris.

BREMER, B. & L. STRUWE (1992): Phylogeny of the Rubiaceae and the Loganiaceae: congruence or conflict between morphological and molecular data. – Amer. J. Bot. **79**: 1171–1184; Lancaster.

BROTHERUS, V. F. (1924): Musci (Laubmoose). 1. Hälfte. – *In:* ENGLER, A., K. PRANTL (eds.): Die natürlichen Pflanzenfamilien. – Pp. 1–478; Leipzig.

– (1925): Musci (Laubmoose). 2. Hälfte. – *In:* ENGLER, A., K. PRANTL (eds.): Die natürlichen Pflanzenfamilien. – Pp. 1–542; Leipzig.

BUCK, W. R. (1980): A generic revision of the Entodontaceae. – J. Hattori Bot. Lab. **48**: 71–159: Nichinan.

– (1988): Another view of familial delimitation in the Hookeriales. – J. Hattori Bot. Lab. **64**: 29–36; Nichinan.

– (1991): The basis for familial classification of pleurocarpous mosses. – Adv. Bryol. **4**: 169–185; Vaduz.

BUCK, W. R. & H. CRUM (1990): An evaluation of familial limits among the genera traditionally aligned with the Thuidiaceae and Leskeaceae. – Contr. Univ. Michigan Herb. **17**: 55–69; Ann Arbor.

BUCK, W. R. & R. R. IRELAND (1985): A reclassification of the Plagiotheciaceae. – Nova Hedwigia **41**: 89–125; Braunschweig.

BUCK, W. R. & D. H. VITT (1986): Suggestions for a new familial classification of pleurocarpous mosses. – Taxon **35**: 21–60; Utrecht.

CROSBY, M. R. (1974): Toward a revised classification of the Hookeriaceae (Musci). – J. Hattori Bot. Lab. **38**: 129–141; Nichinan.

CRUM, H. (1972): The geographic origins of the mosses of North America's eastern deciduous forest. – J. Hattori Bot. Lab. **35**: 269–298; Nichinan.

– (1991): A partial clarification of the Lembophyllaceae. – J. Hattori Bot. Lab. **69**: 313–322, Nichinan.

ENROTH, J. (1994): On the evolution and circumscription of the Neckeraceae (Musci). – J. Hattori Bot. Lab. **76**: 13–20; Nichinan.

FLEISCHER, M. (1900–1922): Die Musci der Flora von Buitenzorg. Band 1–4. – 1729 pp.; Leiden.

FOREY, P. L., C. J. HUMPHRIES, I. J. KITCHING, R. W. SCOTLAND, D. J. SIEBERT & D. M. WILLIAMS (1992): Cladistics. A practical course in systematics. – XI + 191 pp.; Oxford.

Frahm, J.-P. (1995): Laubmoose. – *In:* Frey, W., J.-P. Frahm, E. Fischer & W. Lobin (eds.): Die Moos- und Farnpflanzen Europas. – Kleine Kryptogamenflora **4**: 121–313; Stuttgart.

Frahm, J.-P. & W. Frey (1987): Mossflora. 2., überarbeitete Auflage. – 525 pp.; Stuttgart.

Grout, A. J. (1908): Some relations between the habitats of mosses and their structure. – Bryologist **11**: 97–100; Brooklyn.

Harvey, P. H. & M. D. Pagel (1991): The comparative method in evolutionary biology Oxford. – 248 pp.; Oxford.

Hedderson, T. A. & R. E. Longton (1996): Life history variation in mosses: water relations, size and phylogeny. – Oikos **77**: 31–43; Lund.

Hedenäs, L. (1987a): North European mosses with axillary rhizoids. – J. Bryol. **14**: 429–439; Oxford.

– (1987b): On the taxonomic position of *Tomentypnum* Loeske. – J. Bryol. **14**: 729–736; Oxford.

– (1989): Some neglected character distribution patterns among the pleurocarpous mosses. – Bryologist **92**: 157–163; College Station.

– (1994): The basal pleurocarpous diplolepidous mosses – a cladistic approach. – Bryologist **97**: 225–243; Omaha.

– (1995): Higher taxonomic level relationships among diplolepidous pleurocarpous mosses – a cladistic overview. – J. Bryol. **18**: 723–781; Leeds.

– (1997a): A partial generic revision of *Campylium* (Musci). – Bryologist **100**: 65–88; Fairfax.

– [1997b ("1996")]: A cladistic evaluation of relationships between the Hookeriales, the Sematophyllaceae and some other taxa. – Lindbergia **21**: 49–82; Odense.

– [1997c ("1996")]: A cladistic overview of the "Hookeriales". – Lindbergia **21**: 107–143; Odense.

– [1998a ("1997")]: An evaluation of phylogenetic relationships among the Thuidiaceae, the Amblystegiaceae, and the temperate members of the Hypnaceae. – Lindbergia **22**: 101–133; Odense.

– (1998b): Cladistic studies on pleurocarpous mosses: Research needs, and use of results. – *In:* Duckett, J. G., N. W. Ashton & J. W. Bates (eds.): Bryology for the twenty first century. –Pp. 125–141; Leeds (Maney & Son and the Bristh Bryological Society).

Hedenäs, L. & A. Kooijman (1996): Phylogeny and habitat adaptations within a monophyletic group of wetland moss genera (Amblystegiaceae). – Pl. Syst. Evol. **199**: 33–52; Wien.

Jensen, C. (1939): Skandinaviens bladmossflora. – 535 pp.; Copenhagen.

Limpricht, K. G. (1890–1895): Die Laubmoose Deutschlands, Oesterreichs und der Schweiz. II. Abtheilung. – 853 pp.; Leipzig.

– (1895–1904): Die Laubmoose Deutschlands, Oesterreichs und der Schweiz. III. Abtheilung. – 864 + 79 pp.; Leipzig.

Maschke, J. (1976): Taxonomische Revision der Laubmoosgattung *Myurium* (Pterobryaceae). – Bryophyt. Biblioth. **6**: 1–218; Vaduz.

Miller, H. A. (1971): An overview of the Hookeriales. – Phytologia **21**: 243–252; Plainfield.

Mishler, B. D. (1986): A Hennigian approach to bryophyte phylogeny. – J. Bryol. **14**: 71–81; Oxford.

Nishimura, N., M. Higuchi, T. Seki & H. Ando (1984): Delimitation and subdivision of the moss family Hypnaceae. – J. Hattori Bot. Lab. **55**: 227–234; Nichinan.

Nyholm, E. (1960): Illustrated moss flora of Fennoscandia, II. Musci. Fasc. **4**. – Pp. 287–408; Lund.

– (1965): Illustrated moss flora of Fennoscandia, II. Musci. Fasc. **5**. – Pp. 407–647; Lund.

Ochyra, R. (1989): Animadversions on the moss genus *Cratoneuron* (Sull.) Spruce. – J. Hattori Bot. Lab. **67**: 203–242; Nichinan.

Proctor, M. C. F. (1984): 2. Structure and ecological adaptation. – *In:* Dyer, A. F. & J. G. Duckett (eds.): The experimental biology of bryophytes. – Pp. 9–37; London.

Robinson, H. (1986): On the relationships of the Hookeriaceae. – Bryol. Times **35**: 2–3; Utrecht.

Rohrer, J. R. (1985a): A phenetic and phylogenetic analysis of the Hylocomiaceae and Rhytidiaceae. – J. Hattori Bot. Lab. **59**: 185–240; Nichinan.

– (1985b): A generic revision of the Hylocomiaceae. – J. Hattori Bot. Lab. **59**: 241–278; Nichinan.

Shaw, J. & H. Robinson (1984): On the development, evolution and function of peristomes in mosses. – J. Hattori Bot. Lab. **57**: 319–335; Nichinan.

Smith, A. J. E. (1978): The moss flora of Britain and Ireland. – 706 pp.; Cambridge.

Thiers, B. M. (1988): Morphological adaptations of the Jungermanniales (Hepaticae) to the tropical rain forest habitat. – J. Hattori Bot. Lab. **64**: 5–14; Nichinan.

Vitt, D. H. (1981): Adaptive modes of the moss sporophyte. – Bryologist **84**: 166–186; Carbondale.

Wanntorp, H.-E. (1983): Historical constraints in adaptation theory: traits and non-traits. – Oikos. **41**: 157–160; Lund.

Whittemore, A. & B. Allen (1989): The systematic position of *Adelothecium* Mitt. and the familial classification of the Hookeriales (Musci). – Bryologist **92**: 261–272; College Station.

Author's address:

Lars Hedenäs, Swedish Museum of Natural History, Department of Cryptogamic Botany, Box 50007, S-104 05 Stockholm, Sweden;
e-mail: lars.hedenas@nrm.se.

ISSN 0341-0145

Schriftleitung: Dr. Wolfgang Seeger, Rosenstein 1, D-70191 Stuttgart
Gesamtherstellung: Gulde-Druck GmbH, D-72072 Tübingen